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# Orthodox seeds and resurrection plants: Two of a kind?[1]

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**Short title: Orthodox seeds and resurrection plants**

**One sentence summary**

Understanding shared strategies for desiccation tolerance in orthodox seeds and resurrection plants can yield insights for agricultural improvement.

**Abstract**

Although staple crops do not survive extended periods of drought, their seeds possess desiccation tolerance (DT), as they survive almost complete dehydration (desiccation) during the late maturation phase of development. Resurrection plants are plant species whose seeds and vegetative tissues are desiccation tolerant. Vegetative DT first arose with the transition from aquatic to terrestrial life forms, but it was lost as plants acquired mechanisms for drought resistance. DT was then confined to seeds, spores, and pollen grains. We review evidence suggesting that angiosperm resurrection plants have reactivated the seed DT program in vegetative tissues. Novel ~omics technologies are providing a better understanding of the

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changes necessary for this reactivation and may aid in the development of crop varieties that are better able to survive extreme drought conditions.

## Information for crop improvement

Climate variability and climate change are associated with the warming and drying of tropical land areas, the main agricultural regions of the world, resulting in reduced carbon uptake by vegetation, increased carbon release by fire, and an increased likelihood of high-precipitation extremes (Iizumi and Ramankutty, 2015; Betts et al., 2016). The association of these factors with the growing population and dietary shifts has increased concerns for global agriculture and food security (Iizumi and Ramankutty, 2015). The prospect of food insecurity raises the need to improve crop yield stability in variable environments, especially by breeding additional drought-tolerant crop varieties (Bansal et al., 2014; Mickelbart et al., 2015). To date, most so-called drought tolerant crops have been bred for improved resistance to water loss under drought conditions. However, under severe and prolonged drought, water loss is inevitable, and such crops fail.

The recent advent of whole genome, transcriptome, metabolome, proteome, and associated technologies offers valuable tools for mining genes and pathways for crop improvement (Bansal et al., 2014). Current and rapidly emerging technologies, such as genome-editing tools (e.g., zinc-finger nucleases [ZFNs], transcription activator-like effector nucleases [TALENs], and clustered regularly interspaced short palindromic repeat [CRISPR/Cas system]), high-throughput phenomics, RNAi, and marker-assisted breeding enable robust genetic engineering in many plant species (Bansal et al., 2014; Araki and Ishii, 2015). Selective breeding using natural genetic variation that reflects the evolution of plants within diverse ecological niches has already been performed successfully (Mickelbart et al., 2015). However, more models are needed to guide efforts to transfer genomics information from non-crop, well-adapted plant species to crops (Langridge and Reynolds, 2015).

In this context, investigating **desiccation tolerance** (DT, see Box 1) and **resurrection plants** (see Box 1) is a promising way to facilitate the breeding of plants with improved tolerance to water deficit in their tissues, as typically imposed by severe drought. Phylogenetic evidence suggests that vegetative DT in angiosperm resurrection plants represents an adaptation of developmentally regulated DT mechanisms in seeds that have been adjusted to the whole plant context (Oliver et al., 2000; Illing et al., 2005; Rascio and Rocca, 2005; Bartels and Hussain,

2011; Farrant and Moore, 2011; Farrant et al., 2015; Costa et al., 2017). Some similarities between seeds and angiosperm resurrection plants have been analyzed in the past (Illing et al., 2005), and the availability of more comprehensive desiccation-associated transcriptomes from resurrection plants (Rodriguez et al., 2010; Bartels and Hussain, 2011; Yobi, et al., 2017) linked to sequenced genomes (Xiao et al., 2015; Costa et al., 2017) and seedlings in which DT is re-introduced (Maia et al., 2011; Terrasson et al., 2013; Costa et al., 2015) is allowing the exact mechanisms inherited by these plants to be refined. For example, a cross-species comparison of DT-related transcriptomes revealed a considerable similarity in the genes involved in vegetative DT and seed DT (Costa et al., 2016). Transcripts of homologs of a seed-specific *Arabidopsis thaliana* 1-Cys peroxiredoxin gene (Haslekås et al., 1998) accumulate in the leaves of various resurrection plants in response to dehydration (Mowla et al., 2002; Yobi et al., 2017). An analysis of the genome of the resurrection species *Xerophyta viscosa*, along with transcriptomic changes that occur during desiccation and rehydration, indicated that transcripts typically associated with seed DT were induced, such as homologs of the transcription factor gene ***ABSCISIC ACID INSENSITIVE 3*** (***ABI3,*** see Box 1) (Costa et al., 2017). The lack of DT-specific genome organizational features in the resurrection species *Boea hygrometrica* supports the notion that vegetative DT evolved from pre-existing genetic modules (Xiao et al., 2015).

Considering that staple crops have the genes necessary for DT (as they produce desiccation-tolerant seeds despite not surviving extended periods of drought), understanding how angiosperms can be "converted" from being desiccation-sensitive to -tolerant will provide the resources necessary for biotechnological improvement of stress tolerance in agricultural crops and the production of **extremophile crops** (see Box 1) (Barak and Farrant, 2016). The key factor for this conversion may be the similarity between seed DT and vegetative DT. Although in desiccation-tolerant life forms, there is often a trade-off between productivity and survival when the organism enters a quiescent state under severe water-deficit conditions, these organisms also activate downstream effectors of water deficit tolerance (Berger et al., 2016). These downstream effectors, which are shared by desiccation-tolerant seeds and vegetative tissues, represent promising resources for improving water-deficit tolerance in crops, as they increase the amount of water loss tolerated before growth ceases.

## Plant evolution and DT

It is likely that the first organisms to transition from fully aquatic habitats to a sub-aerial existence were photosynthetic prokaryotes such as cyanobacteria, followed by fully aquatic eukaryotic algae adapted to life in muddy lake margins (Graham et al., 2012; Graham et al., 2014). These algae occurred in organic-poor soils, with reduced accessibility to water and excess light, where they had to distinguish between sub-aerial and aquatic conditions and adjust their developmental processes and body morphology accordingly and reversibly (Graham et al., 2012; Graham et al., 2014). DT allowed these algae to more effectively adapt to habitats and periods of limited hydration. Therefore, DT evolved during the water-to-land transition and was carried forward together with other physiological traits useful in terrestrial habitats, such as the production of resistant walls by vegetative cells, which reduce UV- and desiccation-induced cellular damage (Graham et al., 2012).

Later, during the evolution of vascular plants, the first mechanisms acquired for **drought resistance** (see Box 1) were the acquisition of a vascular system and a waxy cuticle with stomata by sporophytes, allowing them to minimize and regulate water loss from aerial tissues (Watkins et al., 2007). Resisting drought allowed these plants to invest more time and energy into growth and reproduction, overcoming the slow growth associated with DT. Less than 1% of the sporophytes of modern pteridophytes are desiccation tolerant (Pittermann et al., 2013). On the other hand, DT is widespread in the gametophytes of pteridophytes. These gametophytes lack vascular tissues and have a poorly developed cuticle, resembling bryophytes (Watkins et al., 2007). An example of this transition is the fern *Mohria caffrorum*, which produces desiccation-tolerant spores on a desiccation-sensitive frond (Farrant et al., 2009).

The survival of seed plants over both short- and long-term drought was further improved by the evolution of stomatal regulation via abscisic acid (ABA) (Mcadam and Brodribb, 2013), favoring the confinement of DT to pollen grains, spores, and seeds. Later, during the evolution of angiosperms, resurrection plants reacquired DT in their vegetative tissues through a myriad of

genetic changes in at least 13 separate lineages (Oliver et al., 2005; Porembski, 2011; Gaff and Oliver, 2013). These lineages correspond to the angiosperm families containing resurrection species (Oliver et al., 2005; Gaff and Oliver, 2013). Interestingly, these families are not in a linear phylogenetic sequence from one to the other, and except for Myrothamnaceae and Velloziaceae, only a small portion of the species in each family possess vegetative DT (Gaff and Oliver, 2013).

Transposable element (TE) amplification and chromosomal rearrangements, including duplication, inversions, and translocations, are the main mechanisms for plant genome evolution, influencing one another and reinforcing their potential to drive genome evolution and to generate genetic novelty (Bennetzen and Wang, 2014; Vicient and Casacuberta, 2017). Genomic evidence indicates that different changes have taken place behind the evolution of each resurrection plant lineage. For instance, the percentage of the genome that accounts for TEs is surprisingly low in *X. viscosa* (18%) (Costa et al., 2017) compared to *Oropetium thomaeum* (75%) (VanBuren et al., 2015) and *B. hygrometrica* (43%) (Xiao et al., 2015). The types of genome duplication events that contributed to the number of genes encoding the protective **late embryogenesis abundant** (LEA) **proteins** (see Box 1) in angiosperm resurrection plants also differ: whole genome duplications played critical roles in *X. viscosa*, while in *O. thomaeum* and *B. hygrometrica*, dispersed duplications were more crucial (Costa et al., 2017). An analysis of gene families that expanded and contracted in *X. viscosa* in relation to 15 other plant genomes, including *O. thomaeum*, indicated a small overlap in the gene families that expanded and contracted in only these two resurrection species (Costa et al., 2017). A large fraction of the contigs assembled from hydrated, dehydrated, desiccated, and rehydrated samples of the resurrection species *Sporobolus stapfianus* (Yobi et al., 2017), *Craterostigma plantagineum* (Giarola and Bartels, 2015), and *Haberlea rhodopensis* (Gechev et al., 2013) predict the presence of protein sequences that bear little or no similarity to proteins in public databanks. Orphan or taxonomically restricted genes are genes without known homologs that either evolved *de novo* from non-coding sequences or were derived from older coding material (Arendsee et al., 2014). Whereas ~29% of annotated genes in *B. hygrometrica* are orphan genes (Xiao et al., 2015), only 5.4% in *X. viscosa* are orphan genes, with 5–15% being fairly typical in various species (Arendsee et al., 2014). These findings suggest that the acquisition of vegetative DT in *X. viscosa* relied more on the redirection

of genetic information than on the genesis of novel genes. An analysis of two orphan genes from *C. plantagineum* (a cysteine-rich rehydration-responsive protein 1 gene [*CpCRP1*] and an early dehydration-responsive protein 1 gene [*CpERD1*]) involved in the dehydration/rehydration cycle suggested recent, family-specific evolution of these two genes (Giarola et al., 2014). This finding suggests that different genetic architectures underlie the resurrection phenotype, and it supports the notion that independent evolutionary events led plants to reacquire vegetative DT (Gaff and Oliver, 2013).

**Seed DT vs. vegetative DT**

Orthodox seeds acquire DT during the late maturation phase of development and lose it during germination. Yet, there is a small developmental window during which DT can be rescued by treatment with ABA and/or an osmoticum (reviewed by Dekkers et al., 2015). In short, these treatments induce growth arrest, activate protective mechanisms, inhibit metabolism, and promote adaptation to stress conditions. Notably, the ability to re-induce DT in germinated seeds is dependent on developmental stage, and after the DT window closes, the germinated seeds become irreversibly sensitive to desiccation (Dekkers et al., 2015). For *A. thaliana*, this stage coincides with the appearance of the first root hairs (Maia et al., 2011) and for *Medicago truncatula*, it coincides with a radicle length between 1 and 3 mm (Buitink et al., 2003). *X. viscosa* also produces orthodox seeds that give rise to seedlings displaying a window of desiccation sensitivity to fast drying prior to the acquisition of DT at a later vegetative stage (Costa et al., 2017). ABA treatment is an effective way to establish DT in these seedlings through inducting similar responses to those observed in germinated seeds, as described above. Therefore, desiccation-sensitive *X. viscosa* seedlings resemble newly germinated orthodox seeds during the DT-reinduction window.

Since angiosperm resurrection plants produce DT seeds, the genetic mechanisms of the latter are likely the source of genetic reprogramming for the evolution of all angiosperm resurrection plants (Oliver et al., 2000). Hence, the same key traits are shared by vegetative DT and seed DT: (1) regulated shutdown of photosynthesis in poikilochlorophyllous resurrection plants; (2) mechanisms to protect against water loss and to institute a slow drying rate; (3)

maintenance of cell integrity via the accumulation of (solid) compounds; (4) modification of cell wall plasticity/elasticity; (5) mechanisms for longevity in the dry state; and (6) the involvement of ABI3.

*Regulated shutdown of photosynthesis in poikilochlorophyllous resurrection plants*

A major potential source of damage to desiccating green tissues is photosynthesis. The uncoupling of carbon fixation from electron transport results in the generation of massive amounts of reactive oxygen species (ROS) (Figure 1, reviewed by (Challabathula et al., 2016; Rogers and Munné-Bosch, 2016)). **Homoiochlorophyllous resurrection plants** (**HDT**, see Box 1, Figure 1), such as *B. hygrometrica*, *Craterostigma* sp., *H. rhodopensis*, *Myrothamnus flabellifolius*, *S. stapfianus*, and *Tripogon loliiformis*, degrade only a small amount of chlorophyll (Chl) during dehydration (Farrant, 2000; Georgieva et al., 2007; Blomstedt et al., 2010; Mitra et al., 2013; Sárvári et al., 2014; Williams et al., 2015). These plants retain macro-level thylakoid structure, deactivating and activating partial components of the photosynthetic machinery in a specific order, which allows for coordinated shut down and subsequent reinstatement of photosynthesis during drying and rehydration, respectively (Charuvi et al., 2015; Zia et al., 2016). In HDT, leaf area is reduced upon exposure to light via (for example) leaf curling, the presence of reflective hairs, and anthocyanin accumulation (Figure 1) (Challabathula et al., 2016; Farrant et al., 2017). On the other hand, under dehydration stress, **poikilochlorophyllous resurrection plants** (**PDT**, see Box 1, Figure 1), such as *Xerophyta humilis* and *X. viscosa*, gradually dismantle their photosynthetic machinery, leading to almost Chl-free dehydrated leaves (Figure 2) (Porembski, 2011; Tuba and Lichtenthaler, 2011; Beckett et al., 2012; Christ et al., 2014). In both *X. humilis and X. viscosa*, Chl degradation begins once leaf water content decreases below 80% RWC (relative water content) and continues to depletion in the air-dry state. During rehydration, Chl biosynthesis is rapidly induced, and the regeneration of thylakoids is apparent within 3 days (Ingle et al., 2008; Christ et al., 2014). This poikilochlorophyllous mechanism bears a strong resemblance to the degradation of Chl in maturing seeds. In PDT, Chl, LHCb1 (a component of the light harvesting antennae of photosystem II [PSII]) and PsbA (a subunit of the core complex of PSII) are degraded during dehydration and re-synthesized during rehydration, indicating the involvement of the pheophorbide *a* oxygenase (PAO)/phyllobilin

pathway (Christ et al., 2014). Chl degradation during seed maturation also follows the PAO/phyllobilin pathway and is partly controlled by ABA through the regulation of *NYC1* (*NON-YELLOW COLORING 1*, encoding a Chl *b* reductase isoform involved in Chl catabolism) expression (Nakajima et al., 2012). In these seeds, chloroplasts are transformed into another type of plastid (e.g., leucoplasts, gerontoplasts), where LHCII (light harvesting complex proteins of PSII) is retained in the remnants of structures that resemble a premature form of thylakoid membranes (Nakajima et al., 2012). When the Chl *b*-to-*a* conversion is suppressed in developing *A. thaliana* seeds, Chl is retained in the embryo, dramatically reducing seed germination capacity (Nakajima et al., 2012).

In both vegetative and seed tissues, Chl retention is associated with low storability. Seeds of *A. thaliana* mutants that do not degrade Chl properly failed to germinate after 23 months of storage, whereas wild-type seeds maintained high germination rates after 42 months of storage (Nakajima et al., 2012). Phytyl tails released as a result of Chl breakdown are thought to serve as a substrate for the biosynthesis of tocopherols (well-known antioxidants involved in seed longevity) (reviewed by Sano et al., 2016). *Craterostigma wilmsii* plants in the dry state under simulated field conditions did not survive for more than three months, whereas 10 months of dry storage did not affect plant survival in *X. humilis* (Bajic, 2006). This difference is, at least in part, due to the accumulated damage to chloroplasts and the loss of repair capacity during dry storage in *C. wilmsii* (Bajic, 2006).

*Mechanisms for protection against water loss and drying rate*

In both seeds and vegetative tissues of angiosperm resurrection plants, most mechanisms associated with subcellular protection against water deficit are induced (reviewed by Farrant et al., 2012; Dinakar and Bartels, 2013; Farrant et al., 2017), rather than being constitutive as is the case in ancestors of land plants (Oliver et al., 2000; Oliver et al., 2005). Thus, the rate of drying is important in the institution of such protection mechanisms. Dehydration during seed maturation is, overall, a slower process than dehydration of PDT tissues. However, if drying of seeds during maturation to water contents below 10% is considered, the drying times are comparable. The initial slow reduction in water content, prior to this, is largely the result of the accumulation of reserves, driving water out of the cells (Angelovici et al., 2010). From the

attainment of maximum dry weight onwards, together with the detachment of seeds from the funiculus connecting them to the mother plant (seed abscission), water loss is the result of environmentally controlled drying. That of vegetative tissues is correlated with water supply via the roots, evapotranspiration rates, and the replacement of water in vacuoles and cytoplasm by various metabolites.

*Maintenance of cell integrity via the accumulation of (solid) compounds*

Water loss leads to cell shrinkage, which induces changes in solute concentration, increases in cytoplasm viscosity, and the "plasticizing" of cell walls (Moore et al., 2013; Walters, 2015; Leprince et al., 2017). The increase in solute concentration and consequent increase in cytoplasmic viscosity are due to the accumulation of sugars, proteins, salts, organic acids, and amino acids. These compounds interact to form stable intracellular glasses, which ensure optimal preservation of cellular components, proteins, and macromolecules in the dry state (Buitink and Leprince, 2004; Walters, 2015; Leprince et al., 2017).

Maturation drying of *A. thaliana* seeds is associated with a major switch in seed metabolism, when the negative trend in changes in metabolite levels during reserve accumulation is partially inverted (Fait et al., 2006). The metabolites involved in this switch are distinct sugars (namely sucrose, galactose, arabinose, trehalose, sorbitol/galactinol, gluconate 6-phosphate, and glycate), organic acids, nitrogen-rich amino acids, and shikimate-derived metabolites (Fait et al., 2006). Resurrection plants also experience a metabolic switch during dehydration. When water content drops below ~55% RWC, stomata close, carbon gain from photosynthesis ceases, and metabolism shifts from normal growth to cell defense and the accumulation of protective molecules, such as sucrose, raffinose-family oligosaccharides, and amino acids (Gechev et al., 2013; Farrant et al., 2015; Mladenov et al., 2015; Yobi et al., 2017). For instance, *H. rhodopensis* leaves start to accumulate sucrose at ~60% RWC during desiccation in parallel with the significant consumption of glycolytic intermediates (Mladenov et al., 2015). In dehydrating leaves of the resurrection species *Barbacenia purpurea*, the metabolic switch occurs under high water contents, when RWC drops below 60–70%. At this point, the levels of polyols, monosaccharides, sucrose, and raffinose-family oligosaccharides increase, while the levels of shikimic acid and starch decrease (Suguiyama et al., 2014).

The maintenance of cell integrity is also achieved through changes in the surface-to-volume ratios of vacuoles, thereby preventing extensive folding of the tonoplast and irreversible fusion of tonoplasts during desiccation (Farrant, 2000; Farrant et al., 2007; Karbaschi et al., 2015). To achieve this change, the central vacuole fragments form small vacuoles filled with storage compounds (Figure 2). In seeds, these vacuoles are typically filled with storage proteins by the end of seed filling, when late maturation starts and water content decreases markedly (Fait et al., 2006; Verdier et al., 2013; Leprince et al., 2017). The protein storage vacuoles found in orthodox seeds are thought to be very similar to the vacuoles found in resurrection plants, although the nature of the contents can differ among species (Figure 2) (reviewed by Farrant et al., 2017). For example, in the resurrection species *Eragrostis nindensis*, vacuoles are filled with some protein as well as a number of metabolites (Willigen et al., 2004), whereas in *M. flabellifolius*, the vacuolar content is thought to almost exclusively consist of a polyphenol that also has a powerful antioxidant effect (Moore et al., 2007). These small vacuoles show higher mechanical stability than large vacuoles, thereby minimizing mechanical stress (Rascio and Rocca, 2005)

*Modification of cell wall plasticity/elasticity*

In addition to the alleviation of mechanical stress via water replacement as described above, changes in cell wall plasticity and architecture during drying can significantly help minimize the stress associated with the loss of turgor pressure (Moore et al., 2008; Moore et al., 2013). The use of arabinose-containing polymers and the arabinosylation of existing polymers upon water loss in the cell walls of seeds and resurrection plants "plasticize" the cell wall and prevent polymer aggregation (reviewed by Moore et al., 2013). Besides increasing the plasticity and/or fluidity of cell walls, these plasticizers function as "mechanosensors" in water loss signal perception (Moore et al., 2013).

Cell walls in seeds dry out during maturation, and a number of these walls contain higher arabinan levels than the vegetative tissues of the mother plant (Gomez et al., 2009; Tenhaken, 2015). During germination, the arabinan is metabolized and generates the precursors required for the biosynthesis of wall polymers and arabinogalactan proteins (Gomez et al., 2009; Tenhaken, 2015). Large quantities of arabinans found in maturing *A. thaliana* seeds are degraded during

germination, suggesting they play a role in seed desiccation and are metabolized after germination, as they are no longer required (Gomez et al., 2009).

Although resurrection plants from different lineages have evolved "wall-specific" solutions to desiccation, those that have been characterized use (or appear to use) some arabinose-containing polymers (Moore et al., 2013). At the transcriptional level, hydrated *C. plantagineum* leaves are enriched in the transcripts of genes involved in cell wall remodeling and the maintenance of cell wall plasticity, possibly to ensure timely increases in cell wall flexibility and to prevent mechanical strain upon dehydration (Rodriguez et al., 2010). The transcription of *HrhDR35* (*DESICCATION-REGULATED 35*), encoding a putative xyloglucan endotransglucosylase/hydrolase involved in cell wall modification, is rapidly induced in dehydrating *H. rhodopensis* leaves (Georgieva et al., 2012).

*Mechanisms for longevity in the dry state*

Mechanisms for longevity in the dry state provide stabilization of the biological entity for long periods of time by slowing down deteriorative reactions (Buitink and Leprince, 2004; Chatelain et al., 2012). As discussed above, Chl degradation and changes in the proportion of arabinose in the cell wall are highly correlated with longevity in resurrection plants and seeds. However, additional mechanisms involved in longevity in the dry state are shared by orthodox seeds and angiosperm resurrection plants.

During early seed development, the innermost seed layer (endothelium) accumulates polymeric flavonoids that become oxidized to brown pigments during seed desiccation, providing protection from damage caused by excess light (Rajjou and Debeaujon, 2008). Dehydrating leaves of HDT accumulate anthocyanins, which may help protect the plant against excess light (Figure 1) (Sherwin and Farrant, 1998). In addition to their role as sunscreens, these pigments scavenge ROS and therefore limit oxidative stress, hence increasing longevity (Rajjou and Debeaujon, 2008). The reduced longevity in dry HDT compared to PDT might be due to the degradation of anthocyanins, causing great ROS-induced damage to the outer leaves and exposing the more susceptible inner leaves to damage (Bajic, 2006).

Although ROS may act as signaling molecules to regulate biological processes, they also damage cellular components and reduce longevity in the dry state (Wang et al., 2015; Sano et al., 2016). Therefore, ROS levels must be tightly controlled in the cell via enzymatic and non-enzymatic ROS scavenging systems (Wang et al., 2015; Sano et al., 2016). Seeds and resurrection plants use a complex array of inherent antioxidant molecules to protect themselves from abiotic stress, such as superoxide dismutases, catalases, glutathione- and ascorbate peroxidases, flavonoids, and tocopherols (Illing et al., 2005; Djilianov et al., 2011; Dinakar and Bartels, 2012; Gechev et al., 2013; Sano et al., 2016; Farrant et al., 2017). In angiosperm resurrection plants, genes encoding antioxidant enzymes are either constitutively expressed or induced by drought (~50% RWC), particularly desiccation (Dinakar and Bartels, 2012; Gechev et al., 2013; Farrant et al., 2015). In the angiosperm resurrection species *Ramonda nathaliae* (an HDT), a time-course analysis of different antioxidant enzyme activities revealed the sequential involvement of these enzymes in dehydration and subsequent rehydration (Jovanović et al., 2011).

LEA proteins contribute to the stability of intracellular glasses and therefore to DT and survival in the dry state (Buitink and Leprince, 2004; Popova et al., 2015). LEA protein levels in maturing *A. thaliana* and *M. truncatula* seeds are positively correlated with an increase in seed longevity (Hundertmark et al., 2011; Chatelain et al., 2012). In *A. thaliana* seeds and *X. viscosa* leaves, LEA proteins are broadly distributed in subcellular compartments, reflecting their protective role of the various cellular membranes (Candat et al., 2014; Costa et al., 2017). LEA genes are dehydration-inducible and are constitutively expressed in resurrection species (Rodriguez et al., 2010; Jovanović et al., 2011; Gechev et al., 2013; Giarola et al., 2015; Costa et al., 2017). The expression of LEA genes from *C. plantagineum* increases upon early or partial dehydration (Rodriguez et al., 2010; Giarola et al., 2015). A genome-wide search for LEA proteins in *X. viscosa* identified 126 LEA motif-containing proteins, 90 of which are differentially expressed during dehydration and rehydration (Costa et al., 2017). This number is significantly higher than that identified from the genomes of 25 other angiosperm plant species, including two resurrection species (Costa et al., 2017).

*Involvement of ABI3*

342 The acquisition of vegetative DT by angiosperm resurrection plants is mediated by
343 changes in gene expression and the adaptation of seed DT to the whole plant context (Gaff and
344 Oliver, 2013). ABI3 was originally discovered as a seed-specific transcription factor but has
345 since been shown to function in abiotic stress responses in the vegetative tissues of desiccation
346 tolerant and -sensitive angiosperm plants (Khandelwal et al., 2010; Mönke et al., 2012; Delahaie
347 et al., 2013; Bedi et al., 2016). In *A. thaliana,* ABI3 controls the middle to late stages of embryo
348 maturation, the acquisition of seed DT, and the expression of several genes, including LEA
349 genes, especially during stress recovery (Delmas et al., 2013; Bedi et al., 2016). Mature seeds of
350 *M. truncatula abi3* mutants are desiccation sensitive (Delahaie et al., 2013). Structural homologs
351 of *ABI3* have been identified in angiosperm resurrection species (Bartels and Salamini, 2001;
352 Costa et al., 2017). A structural homolog of *ABI3* isolated from *C. plantagineum* and its product
353 were able to transactivate LEA genes in transient expression assays, even though its expression
354 was not detected in mature leaves of *C. plantagineum* (Bartels and Salamini, 2001). Although the
355 expression of the two structural homolog of *ABI3* identified in *X. viscosa* do not change in
356 response to leaf desiccation, structural homologs of members of the *ABI3* regulon in *A. thaliana*
357 are tightly co-expressed (Costa et al., 2017). Gene ontology terms over-represented in the ABI3
358 targets in *A. thaliana* are related to embryo, seed, and fruit development, lipid storage,
359 germination, and seedling development (Mönke et al., 2012). By contrast, gene ontology terms
360 over-represented in the structural homologs of these genes in *X. viscosa* are related to more
361 diverse processes, such as metabolic processes (*alcohol metabolic process, cellular carbohydrate*
362 *metabolic process, cofactor metabolic process*, and *tetraterpenoid metabolic process*) and
363 photosynthesis (*plastid organization, regulation of photosynthesis*, and *stomatal complex*
364 *morphogenesis*) (Costa et al., 2017).

365

366 **Concluding Remarks**

367 In seeds, there is a considerable overlap in the sets of genes associated with DT,
368 dormancy, and more general stress responses (Costa et al., 2015) (see Outstanding Questions
369 Box). These gene sets largely overlap with development/maturation-associated gene sets and, in
370 general, may be markers for embryonic cell development. Although some of these genes are

considered “seed-specific”, we have shown that the mechanisms involving these genes are also active in angiosperm resurrection plants. It is therefore tempting to speculate that resurrection plants also bear embryonic identity, which might be a key factor in the similarity between seeds and resurrection plants (see Outstanding Questions Box). In this sense, the embryos of orthodox seeds may be thought of as tiny resurrection plants that lose DT upon germination and, unlike true resurrection plants, do not recover it further during development, except during a narrow window upon germination.

Breeding for drought tolerance or avoidance has proven to be challenging, at least in part because there are typically many drought survival loci that together impart tolerance in crop plants (Mickelbart et al., 2015). Effective stress adaptation determinants range in function from transcriptional regulators that modulate signaling (such as ABI3) and response networks to effectors, such as antioxidants that limit ROS-associated cellular damage (Mickelbart et al., 2015). In some cases, determinants of yield stability under stress are conserved across species, as exemplified by the mechanisms discussed in this review. Considering that such mechanisms have evolved in nature and are already present in staple crops, they are not subjected to regulatory issues and are thus promising targets for crop improvement (Mickelbart et al., 2015) (see Outstanding Questions Box).

## Figure legends

Figure 1: Summary of differences between angiosperm resurrection plants and desiccation sensitive plants (modified from Williams et al., 2015). Upon dehydration below 80–60% relative water content (RWC), resurrection plants activate a series of protective mechanisms to stop light from reaching chlorophyll using two main strategies, homoiochlorophylly and poikilochlorophylly. In homoiochlorophyllous resurrection plants (HDT), the leaf surface area exposed to light is reduced by curling or folding and the leaf may have reflective hairs and/or waxes that reflect light. In addition, anthocyanin, xanthophyll pigments, and polyphenols accumulate in surfaces that remain exposed to light. In poikilochlorophyllous resurrection plants (PDT), chlorophyll (Chl) is degraded and thylakoid membranes are dismantled upon dehydration. At similar RWCs, photosynthesis fails to be downregulated in desiccation-sensitive

plants and consequently, there is an increase in the levels of reactive oxygen species (ROS), unfolded and damaged proteins, and other cellular toxins. When RWC decreases further (to 60–40%), resurrection plants undergo regulated shutdown of electron transfer and generate a robust antioxidant potential, whereas desiccation-sensitive plants undergo drought-induced leaf senescence and ultimately cell death. (A) Dry adult *Craterostigma pumilum* plant, an example of HDT. Bar = 5 mm. (B) Dry adult *Xerophyta humilis* plant, an example of PDT. Bar = 5 mm. (C) Chloroplast in a dry leaf from *Xerophyta elegans,* an example of HDT. Bar = 1 µm. (D) Chloroplast in a dry leaf from *X. humilis*. Bar = 1 µm. (E) Cell in a dry leaf from desiccation-sensitive *Mohria caffrorum*. Bar = 1 µm. Images C–E were obtained under a LEO Omega 912 Transmission Electron Microscope, analyzed using EasiVision Pro Software (Soft Imaging System GmbH) at an operating voltage of 120 kV, and photographed with a 2k X 2k Proscan Digital Camera.

Figure 2: Transmission Electron Micrograph-based infographic comparing a naturally desiccated leaf mesophyll cell from the angiosperm resurrection species *Eragrostis nindensis* (left) with a cell from a mature, desiccated embryonic axis from the orthodox-seeded species, *Craterostigma pumilum* (right). In both cases, the cytoplasm is highly compact and filled with small vacuoles (V) that alleviate the mechanical stress generated by water loss. In the leaf cell, the vacuoles are filled with electron-transparent compounds that function as a source of stored energy for rehydration. In the seed cell, vacuoles are filled with storage proteins that serve as an energy source for germination. Numerous lightly staining lipid bodies (L) are present in the seed tissues, fulfilling a similar purpose. In the leaf cell, a few darkly staining lipophilic structures (L) are evident that are thought to facilitate membrane re-organization during rehydration. By contrast, plastids (C) in the leaf cell take up considerable cellular area. Thylakoid dismantling and plastoglobules are evident, which are rapidly reassembled during rehydration, with photosynthetic competency restored within 24–48 hours (Ginbot and Farrant, 2011).

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RWC

100%

80%

60%

40%

20%

<10%

Hydrated plant

Dehydration

RESURRECTION PLANTS

DESICCATION SENSITIVE PLANTS

Stop light from reaching chlorophyll

HDT

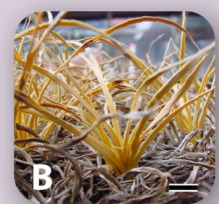
PDT

Reduction of leaf area exposed to light, leaf curling, presence of reflective hairs and accumulation of anthocyanins

Chlorophyll degradation and dismantling of thylakoid membranes


Regulated shutdown of electron transfer

Robust antioxidant potential

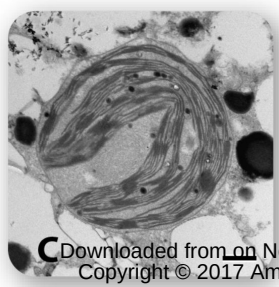


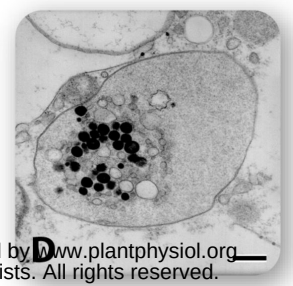

Photosynthesis continues

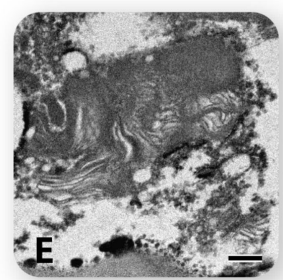
Accumulation of ROS, unfolded proteins and other cellular toxins

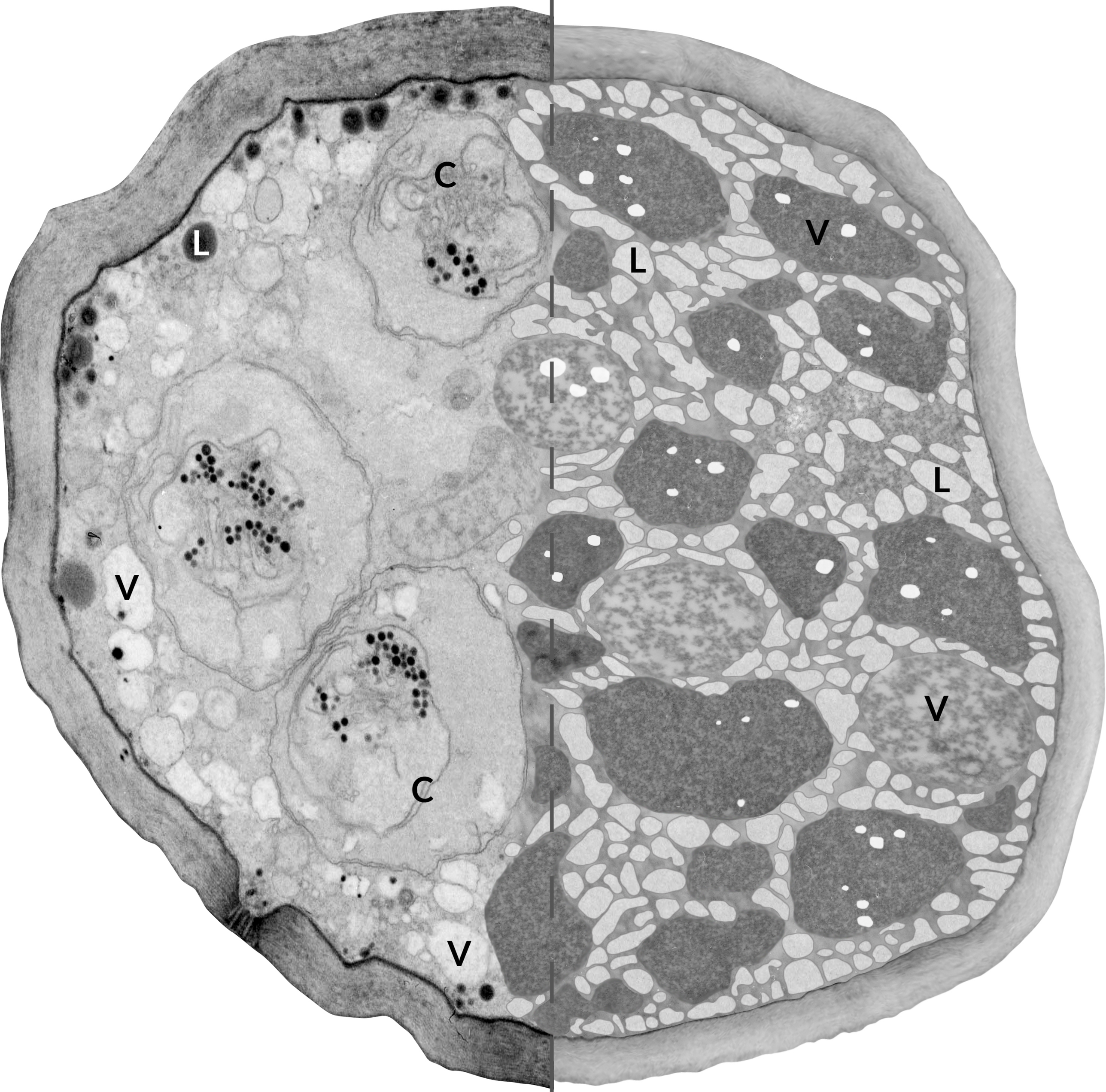
Drought-induced senescence

Cell death





## ADVANCES

- Genome sequence data are shedding light on the different genetic compositions contributing to the evolution of the different lineages of angiosperm resurrection plants.
- Orthodox seeds and angiosperm resurrection plants employ similar mechanisms to deal with extreme water loss.
- Understanding how angiosperm resurrection plants activate seed-associated desiccation tolerance mechanisms in vegetative tissues will provide resources for crop improvement while bypassing issues related to transgenic modification.

## OUTSTANDING QUESTIONS

- How do dormancy-related genes influence the establishment of seed and vegetative DT?
- How do seedlings of resurrection plants enter a desiccation-sensitive window?
- Do all resurrection plants bear embryonic identity?
- Can we identify regulators of gene expression that act exclusively in seed or vegetative DT?
- What is the role played by chromatin organization in modulating DT?
- How can we use resurrection plant traits to modulate the genetic reprogramming involved in vegetative DT to improve drought tolerance in crops whilst minimizing detrimental effects on growth or yield?

## BOX 1. Glossary

**ABI3 (ABSCISIC ACID INSENSITIVE3)**: transcription factor of the plant-specific B3-domain-containing family conserved among angiosperms and nonangiosperms, such as *Physcomitrella patens*. ABI3 contains four conserved domains: the acidic N-terminal domain A1 and three basic domains, B1, B2, and B3. ABI3 was originally characterized as seed specific but is now thought to function in processes beyond seed physiology during abiotic stress, especially desiccation stress signaling.

**Desiccation tolerance**: the ability of certain organisms to tolerate water loss to levels below 0.1 g $H_2O$ per gram dry weight by suspending growth and development yet resuming normal metabolism upon rehydration without accumulating lethal damage.

**Drought resistance**: the ability of some plant species to sustain a certain level of physiological activity in the presence of water shortage. This process combines escape (completion of the life cycle before physiological water deficit occurs), avoidance (prevention of dehydration by minimizing water loss and maximizing water uptake), and tolerance (to low water potential) mechanisms.

**Extremophile crops**: crops able to tolerate and produce a harvestable yield in extreme environments where few other crops can thrive. New extremophile crop varieties should be plastic, as varieties fixed in tolerance tend to perform poorly under good conditions, although they outperform conventional varieties under severe drought conditions. Moreover, they should be able to sacrifice instantaneous transpiration efficiency to maximize growth rates and facilitate drought escape via early completion of their life cycle.

**Homoiochlorophyllous resurrection plants (HDT)**: resurrection plants that retain chlorophyll and thylakoid membrane integrity during drying and thus quickly resume full photosynthetic function when water becomes available.

**Late embryogenesis abundant (LEA) proteins**: natively unfolded, hydrophilic polypeptides with low molecular mass (10–30 kD). LEA proteins protect angiosperm species from damage caused by environmental stresses (e.g., cold, osmotic, and drought stress). LEA proteins were first characterized in seeds during late embryo development, but they have also been found in leaves, roots, and other organs in a variety of organisms, particularly those tolerant of desiccation.

**Poikilochlorophyllous resurrection plants (PDT)**: resurrection plants that lose most of their chlorophyll and dismantle thylakoid membranes during drying, which must be resynthesized upon rehydration.

**Resurrection plants**: a group of land plants that display the remarkable ability to survive desiccation to <5% relative water content for prolonged periods of time. Upon rehydration, these plants rapidly recover full metabolic activity in existing tissues.

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